

Orcinus orca. By John E. Heyning and Marilyn E. Dahlheim

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***Orcinus* Fitzinger, 1860**

Orca Gray, 1846. Generic name preoccupied by *Orca* Wagler, 1830 (= *Hyperoodon*).

Orcinus Fitzinger, 1860. Type species *Delphinus orca* Linnaeus, 1758.

Ophysia Gray, 1868. Type species *Orca capensis* (= *Delphinus orca*).

Gladiator Gray, 1870. Type species *Orca stenorhyncha* (= *Delphinus orca*).

Grampus Iredale and Troughton, 1933 (not Gray). Type species *Delphinus grampus* (= *Delphinus orca*).

CONTEXT AND CONTENT. Order Cetacea, Suborder Odontoceti (considered an order by some authors), Superfamily Delphinoidea, Family Delphinidae. The genus *Orcinus* has been placed in the subfamily Orcininae by several workers. This taxon is not entirely stable in its membership because, in addition to *Orcinus*, it may include *Pseudorca*, *Globicephala*, *Orcaella*, and *Feresa* (Fraser and Purves, 1960; Mead, 1975; Slipper, 1936) or just *Pseudorca* (Kasuya, 1973).

***Orcinus orca* (Linnaeus, 1758)**

Killer Whale

[*Delphinus*] *orca* Linnaeus, 1758:77. Type locality European seas.

Delphinus serra Borowski, 1780:38. Type locality Spitzbergen.

[*Delphinus*] *Gladiator* Bonnaterre, 1789:23. Type locality Spitzbergen.

Delphinus Duhameli Lacépède, 1804:314. Type is description of animal from France.

Delphinus grampus Blainville, 1817:168. Type locality North Atlantic.

Orca Capensis Gray, 1846:34. Type locality Cape of Good Hope.

Delphinus victorini Grill, 1858:21. Type locality Capetown, South Africa.

[*Orca*] *Schlegelii* Lilljeborg, 1866:235. Type locality Norway.

Orca magellanica Burmeister, 1866:99. Type locality south of Buenos Aires, Argentina.

Orca Eschrichtii Reinhardt in Eschricht, 1866:188. Type locality Faeroe Islands.

Orca ater Cope in Scammon, 1869:22. Type based on description of animals from Oregon to Aleutian Islands.

Orca rectipinna Cope in Scammon, 1869:22. Type based on description of animals from California.

Orca stenorhyncha Gray, 1870:71. Type locality English coast.

Orca latirostris Gray, 1870:76. Type locality coast of Essex, North Sea.

Ophysia pacifica Gray, 1870:71. Type locality North Pacific?.

[*Orca*] *pacifica* Gray, 1870:394. Type locality coast of Chile.

Orca africana Gray, 1871:91. Type locality Cape of Good Hope.

Orca tasmanica Gray, 1871:92. Type locality Tasmania.

Orca minor Malm, 1871:81. Type locality Sweden.

Orca antarctica Fischer, 1876:146. Based on drawing.

Orcinus nanus Mikhalev et al., 1981:563. Antarctic waters.

Orcinus glacialis Berzin and Vladimirov, 1983:288. Type locality Indian Ocean sector of Antarctic.

CONTEXT AND CONTENT. Context as above. There are no widely accepted subspecies of *O. orca*.

DIAGNOSIS. *Orcinus orca* is the largest member of the family Delphinidae, with adults ranging in length from 5 to 9 m. The large size, robust body, postocular white spot, and ovate flippers are diagnostic (Fig. 1). Killer whales have proportionately higher dorsal fins than other large delphinids, ranging from one-tenth to one-fifth of the total body length.

There are no comprehensive comparative accounts describing the skulls of large delphinids. The large skull size (condylbasal length to 100 cm), the dental formula (10 to 14/10 to 14) and large teeth distinguish *O. orca* skulls from those of other species, except large false killer whale (*Pseudorca crassidens*) skulls (dental formula 8 to 11/8 to 11; Leatherwood et al., 1982). Skulls of *O. orca* can be distinguished from those of *P. crassidens* by the width across the premaxillaries being less than 50% of rostral width just anterior of antorbital notches and the lateral border of the premaxillaries being slightly more sigmoid in dorsal view and wider distally (Fig. 2). Pterygoids widely separated and teeth compressed anteroposteriorly at the roots are two characteristics often cited as diagnostic for *O. orca* (Glass, 1974), but do not always separate *O. orca* and *P. crassidens*.

The tympanic and periotic bone complex of *O. orca* (Fig. 3)

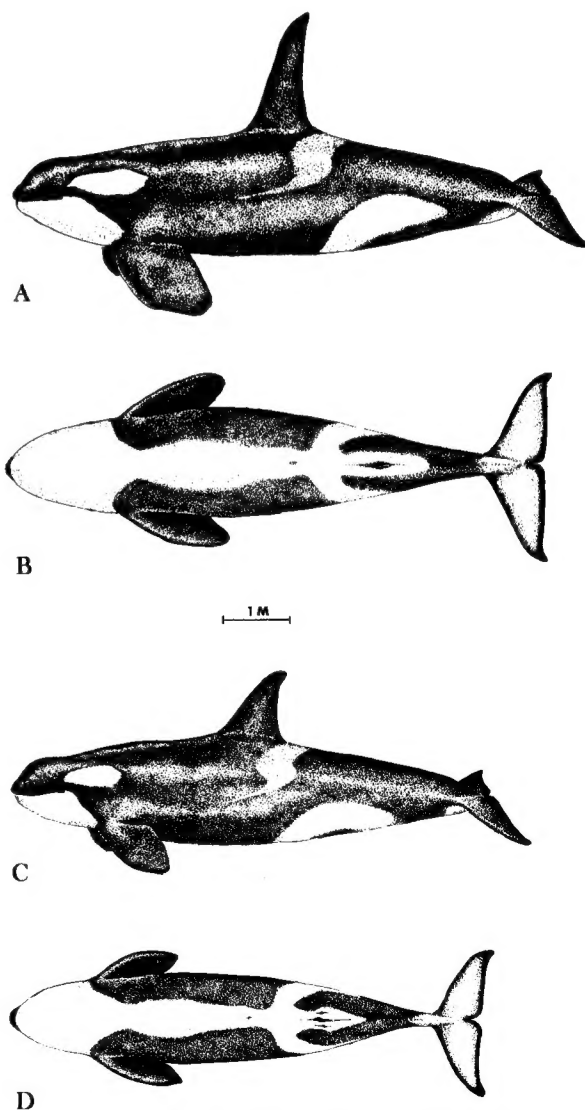


FIG. 1. Lateral and ventral views of a typical adult male (A, B) and female (C, D) of *Orcinus orca*. Illustration by Robin Agoes-Makowski.



FIG. 2. Dorsal, ventral, and lateral views of the skull and lateral view of mandible from a 484-cm male *Orcinus orca* (LACM 52480).

is characterized by a lack of a ventral keel, closure of the elliptical foramen, and massive anterior and posterior processes of the periotic (Kasuya, 1973).

GENERAL CHARACTERS. Female killer whales generally attain a body length of 7.0 m and males 8.2 m (Mitchell, 1975); however, maximum lengths of 8.5 m for females and 9.8 m for males have been reported (Perrin and Reilly, 1984). Killer whales are robust. Few animals have been weighed but a maximum recorded mass was 3,100 kg for a 6.35-m female and 4,000 kg for a 6.04 m male (Hoyt, 1981). The head is blunt with virtually no distinguishable beak. The large (both relatively and absolutely) ovate flippers are positioned about one-fourth the distance from the snout to flukes and contrast with the sickle-shaped flippers of most delphinids. Among males, flippers may measure 2 m (Harmer, 1927) and attain 20% of the body length; among females the flippers attain 11 to 13% of the body length (Eschricht, 1866). Among adult males, the dorsal fin is triangular and may reach 1.8 m in height, whereas in adult females and young males it is less than 0.9 m tall and distinctly falcate. Height of the dorsal fin is a useful character for distinguishing adult males within pods. Sexes of free-living adult females and subadult males are difficult to distinguish.

Killer whales are one of the most strikingly pigmented cetaceans (Fig. 1) making field identification easy. Killer whales are dark, usually jet black, dorsally with a well-demarcated white venter. The

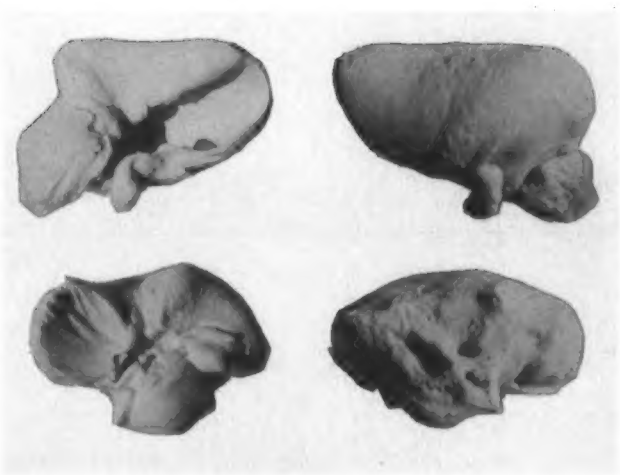


FIG. 3. Upper: dorsal and ventral views of the tympanic bulla; lower: dorsal and ventral views of the periotic of *Orcinus orca* (LACM 52480).

white region typically extends from the entire lower jaw posteriorly, constricting medially between the flippers, then widening slightly and ending just beyond the urogenital region. Continuous with the ventral white area is a lateral flank patch (Mitchell, 1970) that expands dorsoposteriorly above the urogenital region. The ventral aspect of the flukes also are white or light gray. There is a postocular white patch. Light-colored areas often are yellowish, especially in animals from the Antarctic (Berzin and Vladimirov, 1982, 1983; Evans et al., 1982), but yellowish coloration also has been reported from the North Pacific (Scammon, 1874; Scheffer and Slipp, 1948); juveniles tend to be more yellowish than adults. A highly variable gray or white saddle is usually present posterior to the dorsal fin. Melanistic individuals (Scammon, 1874; Scheffer and Slipp, 1948) and partially albinistic animals (Carl, 1960; Scheffer and Slipp, 1948) have been seen in the North Pacific. Individual and geographical variation in the pigmentation pattern exists (Carl, 1946; Evans et al., 1982).

DISTRIBUTION. Killer whales have been observed in all oceans and seas of the world (Fig. 4; Leatherwood and Dahlheim, 1978). Although reported from tropical waters and the open ocean, they seem to be most numerous in colder waters of both hemispheres, with the greatest abundance within 800 km of major continents (Dahlheim, 1981; Mitchell, 1975). In some areas they occur seasonally, but in other areas they are apparently year-round residents.

In the northeastern Pacific Ocean, killer whales occur in the eastern Bering Sea (Braham and Dahlheim, 1982) and have been documented as far north as the Chukchi and Beaufort seas. Animals seem to be abundant off the coast of Alaska with a population estimate of 286 for the Prince William Sound and southeast waters (Leatherwood et al., 1984). Year-round occurrence has been documented for the intracoastal waterways of British Columbia and Washington State where an estimated 260 whales comprising 30 pods have been reported (Bigg, 1982). In the western North Pacific, *Orcinus* occurs frequently along the Soviet coast in the Bering Sea, Sea of Okhotsk (Tomilin, 1957), and off Japan (Kasuya, 1971). Sightings near Hawaii are uncommon (Richards, 1952). Population estimates are not available for the remainder of the North Pacific.

In the North Atlantic Ocean, *O. orca* has been observed off Greenland, Iceland, in the Barents and White seas, and off Novaya Zemlya (Tomilin, 1957). Regular occurrence also is documented off Norway (Jonsgård and Lyshol, 1970), Great Britain, and Ireland (Fraser, 1974; Harmer, 1927). Reports from the Mediterranean are sporadic (Casinos and Vericad, 1976). In the western North Atlantic, sightings have been noted in the Labrador Sea, and off Nova Scotia, Newfoundland, Canada (Sergeant and Fisher, 1957). Sightings decrease southward along the continental United States (True, 1904). There are several records of *O. orca* from Caribbean waters (Caldwell et al., 1971). There are no population estimates for the North Atlantic.

In the southern oceans, killer whales occur to the tip of Tierra del Fuego, South America (Goodall, 1978) and off South Africa

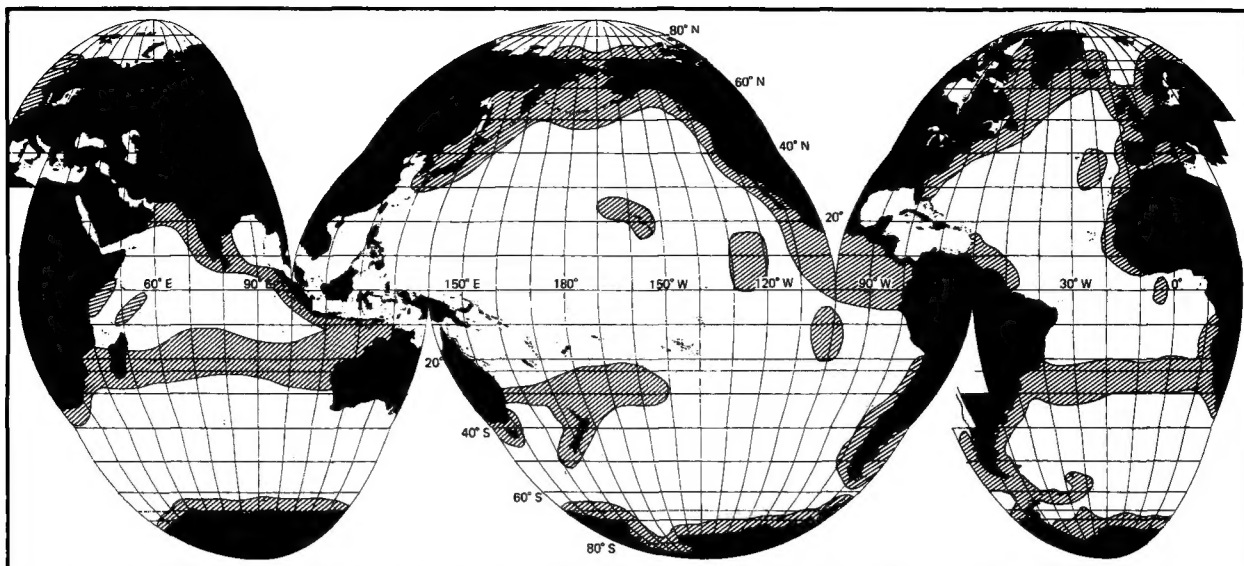


FIG. 4. Geographic distribution of *Orcinus orca*. Shaded areas indicate records of sightings or strandings; however unshaded areas may be part of the normal range with no sightings documented.

(Ross, 1984), but reports decrease northward along the coasts of both continents. They occur at wide intervals in the Indian Ocean. In the South Pacific Ocean, killer whales are recorded from Australia (Bryden, 1978), New Zealand (Baker, 1983) and off the Galapagos Islands (Robinson et al., 1983). In Antarctic waters, *Orcinus* has been recorded as far south as the Ross Sea (Brown et al., 1974, Tomilin, 1957). Their presence has been observed along the edge of the pack ice throughout Antarctic waters (Brown et al., 1974). Despite numerous reports of killer whales in the Southern Hemisphere, details of distribution, movements, and abundance are not known (Dahlheim, 1981).

FOSSIL RECORD. Numerous large delphinoid teeth, primarily from the Pliocene, have been attributed to *Orcinus orca* or a closely related species. Such teeth have been reported from the Pliocene of Italy (Sarrazin, 1933) and Japan (Matsumoto, 1937). *O. semseyi* (Böckh, 1899) from the Lower Miocene strata of Hungary actually is a physeterid. One of the few fossils represented by a good skull is *O. citoniensis* (Capellini, 1883) from the Pliocene of Italy. The specimen consists of a partial skull lacking the posterior and left side of the cranium, but possessing most of the postcranial skeleton. It appears to be a smaller species than *O. orca* with an estimated total length of less than 4 m. *O. citoniensis* has a slightly higher tooth count (14/14) and proportionately smaller teeth than the extant species. In these characters, *O. citoniensis* seems to be intermediate between more typical delphinids and *O. orca* (Pilleri and Pilleri, 1982). An isolated tooth and periotic bone from the Suffolk Crag of England has been referred to *O. citoniensis* (Lydekker, 1887). A dredged fossil jaw of *Orcinus* sp. also has been reported from South Africa (Barnard, 1954).

FORM. The structure of the epidermis of several delphinids including *O. orca* lack the stratum granulosum and stratum lucidum layers, and true keratinization (Harrison and Thurley, 1974). Because the epidermis is sloughed rapidly during swimming, the mitotic division rate is rapid and is 290 times that of epidermis from the human forearm (Harrison and Thurley, 1974). Mean numbers of facial vibrissae ($n = 7$) were 3.6 on the right side and 3.7 on the left (Ling, 1977).

The reported vertebral count is 7 C, 11 to 13 T, 10 to 12 L, and 20 to 24 Ca, total 50 to 54 (Eschricht, 1866; Nishiwaki, 1972). Rib counts range from 11 to 13 per side (Eschricht, 1866) with the anterior six or seven having both capitular and tubercular attachments to the vertebrae and the remainder attached only by the tuberculum. Ribs 1 through 6 attach directly to the sternum. Eschricht (1866) listed the phalangeal formula as I 1, II 4 to 6, III 3 to 4, IV 2 to 3, and V 2, whereas Nishiwaki (1972) reported the count as I 2, II 7, III 5, IV 4, and V 3. Nishiwaki's (1972) higher counts may include the morphologically similar metacarpals as the proximal phalanx of each digit. Ends of phalanges and most carpal

elements were composed of cartilage in an adult male examined by Eschricht (1866). Harmer (1927) hypothesized that the accelerated secondary growth of the flippers in maturing males was related to the continued growth of these cartilages.

Ness (1967) stated that the degree of skull asymmetry in *Orcinus* is low compared with that of other large delphinids. The teeth are relatively large, up to 13 cm in length (Nishiwaki, 1972) and their apices curve inward. Both the mandibular and maxillary aveoli are deep. The teeth are oval in cross-section at the base. Older animals can have extensive wear on the teeth (Caldwell and Brown, 1964).

The entire skeleton is basically built on the typical delphinid plan, but is more robust in all aspects. On the skull, the temporal fossa is noticeably large, indicating a large and powerful temporalis muscle for jaw closure.

The mass of the brain from a 521-cm (curvilinear) specimen was 4,500 g (Caldwell and Brown, 1964). Ridgway and Brownson (1984) estimated an average brain mass of $5,617 \pm 968$ g from animals averaging 555 cm in length. An encephalization quotient of 2.9 for *Orcinus* has been estimated (Ridgway and Brownson, 1984; Wood and Evans, 1980). This encephalization quotient is relatively low for odontocetes, but Wood and Evans (1980) believe this low number may be biased because of the large size of killer whales and their high body weight caused by blubber.

The digestive system is similar to that of other delphinids. The intestines of one animal were 54.2 m long (Eschricht, 1866). The tongue reportedly is protrusible in contrast to the tongue in *Tursiops truncatus* (Donaldson, 1977). Cave (1977) found that the reniculi of the kidney in *O. orca* are arranged in groups of four that are contiguous. The venous return from the kidney differs from that of *Hyperoodon* as the renicular vein receives directly the intrarenicular and centripetal tributaries and no peripheral venous plexus is formed.

Mead (1975) found that, in general, *O. orca* facial anatomy differed little from the typical delphinid plan of asymmetrical nasal sacs except that several structures were proportionately smaller in comparison to 14 other species.

The amino acid sequence of the myoglobin of *O. orca* is more similar to that of *Globicephala* sp. than to the myoglobin of other small delphinids and phocoenids examined (Meuth et al., 1981).

FUNCTION. A lung tidal volume of 46.2 l and a tidal flow of 129 l/s were calculated for a 4.3-m female (Spencer et al., 1967). The electrocardiogram of one captive animal showed no P wave, an inverted T wave, and a simple R wave with a surface-breathing heart rate of 60 beats/min that declined to 30 beats/min when submerged (Spencer et al., 1967). The O_2 capacity of the blood is reported to be moderate for cetaceans in comparison with the much greater O_2 capacity of *Kogia* blood (Lenfant, 1969). Human and bovine antibodies cross-react with similar pituitary hormones of *Orcinus* in-

dicating the presence of both lactotrophs and somatotrophs (Schneyer and Odell, 1984).

ONTOGENY AND REPRODUCTION. Breeding cycles seem not to be fixed worldwide with mating and calving seasons often spanning several months. In the northeast Atlantic, mating occurs from late autumn to midwinter (Jonsgård and Lyshoel, 1970). Polygamy undoubtedly exists in killer whales, and there may be some social control of reproduction.

The average size of males at sexual maturity ranges from 5.2 to 6.2 m. An adolescent growth spurt is reported in males from 5.5 to 6.1 m, the time of sexual maturity (Christensen, 1984). Before this, the growth curves from males and females are identical. Harrison et al. (1972) determined from histological examination that a 656-cm individual with testes masses of 3,632 g (R) and 2,270 g (L) was not mature, and a 724-cm animal with 11,400 g (R) and 12,200 g (L) testes was sexually mature. An examination of 57 mature males from the Antarctic indicated an average testis length of 55 cm and a width of 22 cm. The average testis mass was calculated at 10,000 g with a maximum mass of 23,100 g (Mikhalev et al., 1981).

Females attain sexual maturity between a length of 4.6 to 5.4 m (Perrin and Reilly, 1984). Some of this variation is geographic with northeastern Atlantic animals representing the low end and Antarctic animals the high end (Perrin and Reilly, 1984). The size of ovaries from mature killer whales are about 10 to 12 cm by 5 to 7 cm (Mikhalev et al., 1981). A female with a 91-cm fetus had a corpus luteum measuring 7.6 by 5.1 cm (Turner, 1872). A progesterone level of 0.2 to 0.4 ng/ml has been recorded for one female (Kirby and Ridgway, 1984). Estimates of annual pregnancy rates range from 13.7 to 39.2% with the lower estimates probably more reliable; estimates of annual birth rate range from 4 to 5% (Dahlheim, 1981). Estimates of calving intervals range from 3 to 8 years with observational data indicating that the higher estimates are more typical. However, some evidence suggests that the birth rate may be density dependent (Fowler, 1984; Kasuya and Marsh, 1984). The only killer whales to breed in captivity produced calves 19 months apart (Hoyt, 1981). Estimates of the gestation period differ with 15 months the best current estimate (Perrin and Reilly, 1984).

Detailed embryology and placenta morphology of *O. orca* has been described for several fetuses (Guldberg and Nansen, 1894; Turner, 1872). The maximum size of fetuses differs regionally and has been documented as 255 cm for the North Atlantic (Perrin and Reilly, 1984), 274 cm for the North Pacific (Nishiwaki and Handa, 1958), and 250 cm for the Antarctic (Mikhalev et al., 1981). The smallest neonates recorded are 183 cm for the North Atlantic, 228 cm for the North Pacific (Perrin and Reilly, 1984), and 227 cm for the Southern Hemisphere (Ross, 1984).

Weaning is thought to occur when a calf reaches a length of 4.3 m (Nishiwaki and Handa, 1958) with lactation lasting 12 months (Bryden, 1972). However, calves may be dependent for at least 2 years. Sex ratios at birth appear to be 1:1, but overall ratio of males to females has been reported at 0.48:1 and 0.83:1 for the northeast Pacific (Balcomb et al., 1982; Bigg, 1982), and 1.34:1 for the Marion Islands (Condy et al., 1978).

ECOLOGY. Killer whales are top-level marine carnivores and opportunistic feeders with diets that differ seasonally and regionally. Primarily fish eaters, killer whales are known to prey upon other marine mammals and seabirds. Of 362 stomach contents of *O. orca* examined from the Antarctic region, 60% contained only fish with 31% also containing minke whale (*Balaenoptera acutorostrata*), 9% pinnipeds, and 9% with squid (Ivashin, 1981). Examination of contents from killer whale stomachs from the North Pacific yielded, in order of occurrence, squid, fish, cetaceans, pinnipeds, and miscellaneous (Nishiwaki and Handa, 1958). Useful summary tables of *Orcinus* stomach contents by geographical region are provided in Anon. (1982), Gaskin (1982), and Hoyt (1981). Attacks and predation on large whales has given killer whales their vernacular name and incidents are well documented (Andrews, 1914; Eschricht, 1866; Gaskin, 1982; Hancock, 1965; Jonsgård, 1968; Rice, 1968; Scammon, 1874; Tarpy, 1979; Whitehead and Glass, 1985). One often cited misconception is that one *O. orca* was found with 13 whole porpoises and 14 seals in its stomach. Eschricht (1866:159) stated that partially digested remains of these animals were found and later these were misinterpreted as whole animals. Although there are no

documented instances of killer whales eating man, a few unsuccessful attacks have been reported (di Sciara, 1978). The daily food intake is unknown, though Mitchell (1975) estimated that killer whales consume 4% of their body weight per day. In most geographical regions, movements of killer whales seem to be related to movements of their food supply. Sergeant and Fisher (1957) believed movements off eastern Canada were associated with migrations of seals and rorquals. Jonsgård and Lyshoel (1970) concluded that the distribution and migration of killer whales in the northeastern Atlantic seem to be dependent upon migration of herring.

The life span of killer whales was estimated to be 25 years (Jonsgård and Oynes, 1952), but may be as long as 35 to 40 years (Mitchell and Baker, 1980). The age of most odontocetes is determined by sectioning teeth and counting the dentine or cementum layers. Distinct layering of dentine is present in tooth sections from *O. orca*, but numerous accessory layers make them difficult to interpret (Perrin and Myrick, 1980). The relationship of dentine layers to absolute time for *O. orca* is unknown at present. The natural mortality rate of killer whales is not known, but may be approximately 5% per year for the total population based on information concerning life spans.

The following endoparasites are known from *O. orca*: Trematoda, *Fasciola skrjabini*; Cestoda, *Trigonocotyle spasskyi*, *Phyllobothrium* sp.; and Nematoda, *Anasakis simplex* (Dailey and Brownell, 1972). Killer whales are relatively free of external parasites but barnacles (*Xenobalanus* and unidentified) have been observed on the rostrum and trailing edge of the flukes (LACM No. 72550). There are photographs of a remora (Echeneidae) attached to a killer whale (Lockyer, 1979). Diatoms were reported on the skin of Antarctic animals (Hart, 1935). The ectoparasite *Cyamus orcini* has been described from killer whales (Leung, 1970).

The most common disease reported for killer whales is caused by the wearing of teeth resulting in exposure of the pulp cavity. Infection may penetrate through the pulp cavity causing a jaw abscess. Simpson and Gardner (1972) reported frequent abscessed follicles of the vestigial hair on the rostrum of captive animals that eventually spread over the entire skin surface. The cause of death for captive killer whales ($n = 32$) was reported by Greenwood and Taylor (1985) as pneumonia (25%), systemic mycosis (22%), other bacterial infections (15.6%), mediastinal abscess (9.4%), and undiagnosed (28%). Atherosclerosis was found in one stranded animal (Roberts et al., 1965). The rare genetic Chidiak-Higashi syndrome has been documented in a captive killer whale (Haley, 1973).

Effects of environmental pollutants are not known for cetaceans, however, Calambokidis et al. (1984) found high levels of PCBs and DDT in the tissues of killer whales from Washington State waters.

Killer whales have no significant predators other than man. In various parts of the world, killer whales have been hunted for oil and meat, or killed as a potential competitor by fishermen (Dahlheim, 1981). Tomlin (1957) listed the oil yield for *O. orca* as between 750 and 950 kg per animal and Eschricht (1866) noted that 205 l was yielded from a 6.4-m animal. Killer whale oil in Japan is equal in price to sperm whale (*Physeter catodon*) oil. *Orcinus* oil has an acid value of 0.63, saponification value of 211.9, and an iodine value of 86.4 (Nishiwaki and Handa, 1958). The fresh meat of *Orcinus* is used for human consumption in Japan, but old meat and viscera are used as fertilizer or bait (Nishiwaki and Handa, 1958). In Norway, *Orcinus* meat is used only for animal consumption (Jonsgård and Lyshoel, 1970).

From 1962 to 1976, a live-capture fishery was active in Washington State and British Columbia. By 1976, 302 animals were captured, of which 10 died, 55 were kept for public display in oceanaria, and 237 were released (Asper and Cornell, 1977). Bigg and Wolman (1975) provided data on the live-capture fishery in this area from 1962 to 1973 with slightly different numbers. Since 1976, only one live *O. orca* was captured in this region. Beginning in 1976, Iceland became active in the live-capture fishery (Greenwood and Taylor, 1985). Useful tables of data on captive *O. orca* can be found in Hoyt (1981).

BEHAVIOR. Killer whales usually occur in small pods of fewer than 40 individuals. Off Japan, Kasuya (1971) estimated a mean pod size of 6, and a range of 1 to 30. In Alaskan waters, pod size ranged from 1 to 100 animals, with only 1% of these groups containing 20 or more individuals (Braham and Dahlheim, 1982). In the warm temperate and tropical eastern Pacific, Dahlheim et al.

(1982) noted that pods contained a maximum of 75 animals with a mean of 5.3. An estimated 91% of these pods contained fewer than 10 animals. In the Antarctic, about one-half of the pods had 5 to 10 animals but pods of as many as 100 were observed (Mikhalev et al., 1981). Groups of several hundred animals were observed in Alaskan waters (Braham and Dahlheim, 1982). Large aggregations also were reported from Antarctic and Norwegian waters (Budylenko, 1981; Christensen, 1978). Large groups may reflect a temporary joining of a number of pods possibly related to seasonal peaks in prey availability or possibly social activities. Known multipod gatherings were recorded for waters off southern Vancouver Island, but the biological significance of these large congregations is not understood clearly. Single whales, usually adult males, occur infrequently (Norris and Prescott, 1961). In the Pacific Northwest, the composition of pods seems to remain consistent through time (Bigg, 1982). Approximately 19% of animals within pods were adult males, 40% adult females, and 41% immature whales of both sexes. Pod composition in Alaskan waters was 19% adult males, 55% adult females or subadult males, and 27% juveniles and calves (Leatherwood et al., 1984). No other information on pod composition is available.

Foraging behavior varies; seemingly, it is dependent on the size, number, and type of prey. Off the coast of Argentina, of 568 observations of hunting killer whales, 94% involved cooperative hunting with a 31% success rate, and 64% involved killer whales partially stranding themselves temporarily to capture pinnipeds in the surf (Lopez and Lopez, 1985). Young killer whales are believed to be taught this technique of capturing pinnipeds (Lopez and Lopez, 1985). Evans and Bastian (1969) reported that killer whales circle a school of fish then one or two whales break rank and dash through the middle of the school to feed. In regions of ice, killer whales were observed apparently to peer onto ice floes for seals and sometimes hit the ice from below to knock pinnipeds or penguins (Spheniscidae) into the water (Fraser, 1949). When attacking large whales, killer whales attack in a pack and tear at the whale from several angles. The tongue, lips, and genital region of baleen whales seem to be the primary target of *O. orca*. Killer whales were observed to chase gray whales (*Eschrichtius robustus*) in the Bering Sea. They approached the gray whales initially in a linear formation, then gave pursuit in a loose crescent-shaped formation with the individuals spaced approximately 300 m apart (Ljungblad and Moore, 1983).

In the late 1800's and early 1900's an unusual cooperative relationship between killer whales and shore-based whalers occurred in Australia. Killer whale pods were reported to alert the whalers of the presence of a nearby whale. After killing the whale, the whalers allowed the killer whales to feed upon the tongues of the dead whales (Wellings, 1964).

Norris and Prescott (1961) stated that, in general, animals took three to five short dives of 10 to 35 s duration followed by a longer dive lasting 1 to 4 min. Lenfant (1969) reported that length of dives ranged from 1 to 10 min. *O. orca* has been documented to bowride ships (Dahlheim, 1980). Swimming speeds usually are 6 to 10 km/h; however killer whales can achieve speeds of at least 40 km/h (Lang, 1966). A pod of 15 killer whales was followed and harassed by the RV *Alpha Helix* for 6.5 h during which time the pod retained its structure with the adult males on the wings of a rank-shaped formation, and females and young in the middle (Norris and Dohl, 1980).

Most activities seem to be group oriented (Martinez and Klinghammer, 1969). Care-giving behavior is well documented (Caldwell and Caldwell, 1966; Tomilin, 1957). A partial ethogram is provided by Martinez and Klinghammer (1969) and an overview of *O. orca* behavior in captivity is provided by Defran and Pryor (1980). Aerial behaviors such as breaching, spyhopping, flipper slapping, and lob tailing are common for killer whales. The significance of these behaviors in cetaceans is not known. Killer whales seem to maintain a social hierarchical system. Parallel scars caused by the teeth marks of other killer whales indicate that some intraspecific aggression occurs (Greenwood et al., 1974). Many large delphinids such as *Globicephala* sp. and *Pseudorca crassidens* are well known to mass strand, but similar strandings of several individuals of *O. orca* are not as common (Baker, 1983; Cameron, 1941; Carl, 1946; Dearden, 1958; Eschricht, 1866; Goodall, 1978; Haug and Sandnes, 1982; van Heel, 1962).

Killer whales have an extensive repertoire of sounds with most phonations in the range of 4 to 5 kHz (Dahlheim and Awbrey, 1982). Killer whales are capable of producing two different sounds simultaneously indicating dual sound sources as recorded for *Tursiops*

truncatus. Individual and group differences in signals have been well documented (Dahlheim and Awbrey, 1982; Ford and Fisher, 1982). Recordings from captive animals of known pod origin indicate that pod repertoires are stable over time (Ford and Fisher, 1982). Off British Columbia, individual pods can be identified based solely on dialectal variation (Ford and Fisher, 1982). Pods that associate tend to share certain signals, and those that do not associate or travel together emit different call repertoires. Regional differences in frequency, structure, timing, and call patterns were noted in the Antarctic (Thomas et al., 1981), North Atlantic (Jehl et al., 1980), and the North Pacific (Awbrey et al., 1982). The functional significance of dialects is not known.

Popper (1980) found that among delphinids studied, killer whales have the best absolute acoustical sensitivity, but with a reduced audible frequency range. Hall and Johnson (1971) presented an audiogram of *Orcinus* with a sensitivity range from 500 Hz to 31 kHz with the greatest sensitivity at 15 kHz (-70 ± 5 dB re 1 dyne/cm²). Killer whales are one of the few species of odontocetes that have demonstrated experimentally to be able to echolocate (Diereks et al., 1971). The smallest object that could be discriminated by use of echolocation by a killer whale in captivity was a 10-mm plastic ring, considerably larger than the minimum size of a 2-mm object detected by a *Lagenorhynchus obliquidens* (Popper, 1980). Popper (1980) suggested that killer whales have a diminished use of echolocation and rely more on passive listening.

Underwater visual acuity is reported to be as good as that of pinnipeds and most teleost fish (Dawson, 1980).

GENETICS. The karyotype of the killer whale is $2n = 44$, typical for most cetaceans (Arnason et al., 1980; Duffield-Kulu, 1972). The C-banding pattern differs slightly from other delphinids because of the accumulation of heterochromatin, possibly a recently evolved secondary characteristic (Arnason et al., 1980). The G-banded karyotypes of *O. orca* are similar to the karyotypes of *Tursiops* and *Stenella* sp. (Arnason et al., 1980). Because of conspicuous C-band polymorphism, the karyotype of each specimen was unique (Arnason et al., 1980).

REMARKS. The vernacular name orca is used commonly.

The genus *Orcinus* currently is considered monotypic by most authorities with geographical variation noted in size and color pattern, but a worldwide systematic review is needed. Two recently described Antarctic species, *Orcinus nanus* (Mikhalev et al., 1981) and *O. glacialis* (Berzin and Vladimirov, 1982, 1983), both seem to refer to the same population of smaller individuals that have more yellowish-pigmented light areas. The data presented to support a new species indicate modal differences in several aspects of morphology and ecology, but are based on small samples. Until more substantial data are presented, a conservative view of recognizing only one highly variable species probably is warranted.

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